

Rising Atmospheric Carbon Dioxide and Seed Yield of Soybean Genotypes

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ABSTRACT

If intraspecific variation to rising atmospheric CO₂ exists in soybean [*Glycine max* (L.) Merr.], such variation could be used to select for optimal, high-yielding cultivars. To quantify the range and determine the basis for variation in seed-yield with increasing CO₂, eight ancestral and one modern soybean cultivar differing in determinacy, maturity group, and morphology were grown to reproductive maturity at two CO₂ partial pressures, 40 Pa (ambient) and 71 Pa (elevated). Experiments were replicated three times in temperature controlled glass-houses during 1998 and 1999. Although all cultivars showed a significant increase in seed yield with elevated CO₂, (~40%) Mandarin, an ancestral indeterminate cultivar, showed a greater relative response of seed yield to increased CO₂ than did all other cultivars (~80%). The observed variation in seed yield response to CO₂ was not correlated with any vegetative parameter. At maturity, significant correlations in the relative response of seed yield to CO₂ were observed for both pod weight per plant and seed weight from branches. The later observation suggests that the sensitivity of seed yield response to CO₂ was associated with plasticity in the ability to form new seed in axillary branches in a high CO₂ environment. Genotypic differences in the seed yield response among existing ancestral soybeans suggests that sufficient germplasm is available for breeders to begin selecting lines which maximize soybean yield in response to increasing atmospheric CO₂.

FEW STUDIES have attempted to utilize genotypic variation in the response to increasing atmospheric CO₂ as a means to maximize growth or yield within a given agricultural species. Significant variation in yield by elevated CO₂ has been observed among cultivars of cowpea [*Vigna unguiculata* (L.) Walp.] (Ahmed et al., 1993), rice (*Oryza sativa* L.) (Ziska et al., 1996; Moya et al., 1998), and wheat (*Triticum aestivum* L.) (Manderscheid and Weigel, 1997). Genotypic variation in the response of early growth of tomato (*Lycopersicon esculentum* Mill.) (Lindhout and Pet, 1990) and wild radish (*Raphanus raphanistrum* L.) (Curtis et al., 1994) to elevated CO₂ have also been observed. Heritable variation in the response to elevated CO₂ has, in fact been observed in wild radish with respect to stomatal response (Case et al., 1998). If variation can be exploited to convert additional atmospheric CO₂ into seed yield, then significant increases in productivity could be achieved with relatively low input and minor environmental costs.

It has been argued that empirical selection for yield will automatically select genotypes that are the most responsive to rising atmospheric CO₂ (Kimball, 1985). That is, in the future as atmospheric CO₂ continues to rise, breeders will naturally select the most CO₂ sensitive cultivar. However, it needs to be emphasized that many current cultivars utilized by breeders and growers gener-

ally show less seed yield response than vegetative response with a subsequent decline in apparent harvest index as CO₂ increases (Cure and Acock, 1986; Prior and Rogers, 1995). This has been observed not only for soybean ('Bragg', Baker et al., 1989; 'Fiskeby', 'Clark', Ziska et al., 1998), but also for rice (Moya et al., 1998) and wheat (Manderscheid and Weigel, 1997). This suggests that agronomic cultivars in current use may be ill-suited to maximize the seed yield response with increasing atmospheric CO₂; consequently, evaluation of a wider range of germplasm may be necessary to maximize the seed yield response to future CO₂ levels. At present, no systematic effort to select for CO₂ responsiveness for yield among soybean cultivars has been attempted.

To exploit genotypic variation efficiently, it is necessary to know which physiological or morphological traits are associated with the maximum seed yield response to elevated CO₂. Obviously, the primary basis for the increase in growth and yield is the CO₂-induced stimulation of photosynthesis. However, it can be difficult to predict the response of seed yield from individual leaf measurements since changes in the amount of acclimation or down-regulation can influence the long-term response of photosynthesis to elevated CO₂ (Bunce, 1992).

In contrast to interspecific comparisons (Bunce, 1997), no data have established whether intraspecific variation in growth stimulation by elevated CO₂ is related to differences in photosynthetic response or acclimation, although the possibility cannot be dismissed. Other responses are also affected by CO₂ and could alter the allocation or partitioning of photosynthate among different organs with subsequent effects on photosynthetic acclimation and productivity. In rice for example, the ability to respond reproductively to increased CO₂ in the field is associated with increased tiller formation (Moya et al., 1998). Newer cultivars which limit tillering show a poorer seed yield response to elevated CO₂ (Moya et al., 1998).

One difficulty in selecting soybean genotypes which are CO₂ sensitive is that space and time constraints limit the number of lines which can be examined concurrently at a high CO₂ environment. However, most U.S. genotypes were derived from a small number of ancestral soybean cultivars brought into the USA in the early 1900s (Carter et al., 1993). In the current experiment, we utilize these genotypes (which represent an assortment of morphologies, determinacies, and maturity groups) to assess the sensitivity of seed yield to an enriched CO₂ environment. By using ancestral lines as a starting point, we also attempted to identify characteristics associated with seed yield responsiveness to CO₂.

Abbreviations: AHI, apparent harvest index; DAS, days after sowing; PPFD, photosynthetic photon flux density.

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Given the rapid rate of atmospheric CO₂ increase, and the time necessary for a new cultivar to be developed, quantification of genotypic variation in seed yield and the basis for such variation is a crucial step in any breeding effort to maximize yield with higher atmospheric CO₂.

MATERIALS AND METHODS

Experimental Treatments

Soybean was grown to maturity (March through July, Run 1; July through early December, Run 2; July through December, Run 3) in air-conditioned glasshouses located at Beltsville, MD in 1998 and 1999. Glasshouses were designed to maintain maximum and minimum temperatures between 31 and 17°C, respectively. Air temperature was monitored with shielded, aspirated thermocouples located near the top of each glasshouse. Blowers circulated air continuously through heat exchangers which produced an air speed of ca 0.5 m s⁻¹. Relative humidity inside the glasshouses was not controlled, but was at or near that of ambient outside air. Carbon dioxide partial pressure was controlled 24 h a day by a WMA-2 infra-red analyzer (PP systems, Haverhill, MA) which injected CO₂ if levels dropped below 36 and 70 Pa, respectively, for each glasshouse. The CO₂ treatments were switched between experimental runs to limit microclimate effects. No significant differences in average air temperature were observed during a given experimental run between glasshouses (23.2, 22.9°C; 21.5, 21.2°C and 21.9, 22.0°C for ambient and elevated CO₂ respectively). Average daily photosynthetic photon flux density (PPFD) inside the glasshouses was 21.3, 13.4, and 14.7 mol m⁻² day⁻¹ for Runs 1 to 3 respectively, with no difference in light interception between glasshouses in a given run. No supplemental lighting was used.

A 21x datalogger (Campbell Scientific, Logan, UT) recorded PPFD, temperature and CO₂ partial pressure in both glasshouses at 30-s intervals. Average daytime values of ambient and elevated CO₂ partial pressure were 37.8, 69.1; 37.7, 72.1, and 38.1, 71.2 Pa for Runs 1 through 3, respectively. Average 24-h values were higher than the set point for the ambient CO₂ treatment (43.0, 40.7, and 41.5 Pa for Runs 1–3), because of high (40–50 Pa) ambient nighttime CO₂ experienced at this site (see Ziska et al., 1998).

Cultivars and Growth Conditions

Seed from nine soybean cultivars, (eight ancestral and one modern) were used in all runs (Table 1). These cultivars represent a range of morphologies, indeterminate and determinate types, and maturity groups. All seed was obtained from the USDA Soybean Germplasm collection at Urbana, IL. Three to four seeds per cultivar were sown in either 25- or 30-cm diam pots (20–25 L) filled with vermiculite. For each experiment 10 pots (five of each size) of a given cultivar were assigned to a

CO₂ treatment. Twenty-five-centimeter pots were used for the initial harvest. Plants from a given cultivar were grouped together but groups spaced so as to minimize mutual shading. Plants within a given cultivar were spaced about 30 cm apart. Both individual plants and groups were rotated weekly inside a glasshouse until flowering to minimize border effects. All pots were watered daily to the drip point with a complete nutrient solution containing 13.5 mM nitrogen (ammonium and nitrate, see Robinson, 1984). All pots were thinned to one plant per pot at 10 d after sowing (DAS) in all runs.

Gas Exchange Measurements

Leaf photosynthesis (A, the rate of CO₂ assimilation) was determined for each cultivar at two growth intervals during the vegetative stage. Measurements were made using a differential infra-red CO₂ analyzer and Parkinson chamber (CIRAS-1, PP Systems, Haverhill, MA). Air temperature, humidity and CO₂ partial pressures of the chamber were set to those of the glasshouse. Supplemental lighting was provided and assimilation values reported here were obtained at a PPFD of 1600 μmol m⁻² s⁻¹. Carbon dioxide assimilation was determined for the fully expanded 2nd and 5th leaflet to develop terminally for six plants (three per CO₂ treatment) for each cultivar during Runs 1 and 2. In addition, ambient CO₂-grown leaves were exposed to short-term (10–20 min) increases in CO₂ to elevated (70 Pa) levels. Comparisons between the short-term response of assimilation rate of ambient leaves to elevated CO₂ with the rates of leaves grown and measured at the elevated CO₂ treatment were used to determine the extent of photosynthetic acclimation for each cultivar.

Vegetative and Reproductive Measurements

For all cultivars, the initial sampling to determine growth was at 10 DAS. Subsequent harvests occurred, respectively, with the appearance of initial bloom (31–44 DAS, depending on maturity group) and again at seed maturity (92–121 DAS). Average number of days until flowering was 39, 34, and 35 DAS for Runs 1 to 3. Overall, flowering occurred earlier in Runs 2 and 3 because of shorter days. For a given experiment, no change in days to initial flowering or maturity occurred as a result of CO₂ treatment for a given cultivar. At flowering, five plants for a given cultivar and CO₂ treatment were cut at ground level and separated into leaf laminae, stems (including petioles) and roots. Leaf area was determined photometrically with a leaf area meter (Li 3000, LI-COR, Lincoln, NE). Dry weights were obtained separately for leaves, stems, and roots. The plant parts were dried at 65°C for a minimum of 72 h or until dry weight was constant, and weighed.

Pods were hand harvested at maturity and threshed with a small custom made thresher. Maturity was determined when 95% of the pods on an individual plant had turned brown and vegetative growth had ceased. At maturity, stem weight, pod number, node number, pod weight, axillary branching, and the average weight of 50 seed were obtained for all experimental runs, cultivars and treatments. Because of leaf senescence in soybean, harvest index was calculated as the ratio of seed to stem plus pod biomass at maturity. This is typically done for commercial soybean and is referred to as the apparent harvest index or AHI (Schapaugh and Wilcox, 1980). For Run 3, pods obtained from axillary branches were harvested separately from main stem pods for all treatments.

Statistical Analyses

Because only two glasshouses were available, a randomized complete block design was used with runs over time as replica-

Table 1. Alphabetical list of soybean cultivars used in the study.

Cultivar	Type†	Determinacy	PI	Maturity Group
A.K. Harrow	A	Indeterminate	548298	III
Arksoy	A	Determinate	548438	VI
CNS	A	Determinate	548445	VII
Dunfield	A	Indeterminate	548318	III
Manchu	A	Indeterminate	548365	III
Mandarin	A	Indeterminate	548378	I
Mukden	A	Indeterminate	548391	I
S-100	A	Indeterminate	548488	V
Williams	M	Indeterminate	548631	III

† A refers to ancestral, M to modern genotypes.

tions (blocks). For each run, CO₂ treatment was randomly assigned to a given glasshouse and cultivars randomly assigned within that glasshouse. The entire experiment was replicated three times from 1998 through 1999. The mean value for five plants per CO₂ treatment from a given run was used as a single replicate. The data were analyzed in two ways. For vegetative and reproductive characteristics, the effect of CO₂ partial pressure was tested for individual cultivars by a one-way ANOVA. To examine sensitivity in the responsiveness of seed yield to elevated CO₂ between cultivars, the ratio of the mean value at elevated (E) to that at ambient CO₂ (A) for a given experimental run was calculated with variation among cultivars in this ratio tested using a one way ANOVA. Correlations between the relative seed yield increase with elevated CO₂ and other growth parameters were calculated by simple regression with cultivar means as variables. Unless otherwise indicated, differences were treated as significant at the $P < 0.05$ level.

RESULTS

No significant differences were observed in the absolute rates of leaf assimilation between the 2nd and 5th terminal leaflet at a given CO₂ treatment; consequently, both positions were combined for analysis (Table 2). For all soybean cultivars, exposure to elevated CO₂ resulted in a significant stimulation of leaf photosynthesis, with an average increase of 75% (Table 2). No differences in photosynthetic stimulation were observed between the short- and long-term response to elevated CO₂ for a given cultivar, suggesting that photosynthetic acclimation did not occur during the measurement period (Table 2). The measurement period (i.e., up to the fifth trifoliate) corresponded approximately with the appearance of flowers or early pod fill for all cultivars.

The relative increase in plant biomass in response to elevated CO₂ was less than that observed for leaf photosynthesis, increasing an average of 45% for all cultivars by flowering (Table 3). All ancestral cultivars tested, except for Arksoy, showed a significant increase in total dry weight in response to elevated CO₂. Overall, Harrow had the largest (82%) and Williams had the

Table 2. Single leaf CO₂ assimilation rates for nine soybean cultivars grown at either ambient (40 Pa) or elevated (71 Pa) carbon dioxide partial pressures. Data were taken at full expansion of the 2nd and 5th trifoliate leaves. No differences between the response of trifoliolates was observed, and data were combined for analysis.

Cultivar	CO ₂ concentration, Grown/Measured		
	40/36 Pa	40/71 Pa	71/71 Pa
	μmol m ⁻² s ⁻¹		
Arksoy	26.4b†	39.8a	44.2a
CNS	22.6b	38.2a	39.6a
Dunfield	24.6b	42.9a	44.2a
Harrow	21.0b	39.7a	45.4a
Manchu	19.9b	41.9a	41.5a
Mandarin	27.1b	42.2a	42.4a
Mukden	17.1b	36.4a	33.2a
S-100	25.7b	37.4a	40.4a
Williams	21.4b	44.7a	46.4a
AVERAGE	22.9b	40.4a	41.8a

† Different letters for CO₂ treatments within a cultivar indicate a significant difference at the $P < 0.05$ level according to Student-Newman-Keuls test. Data were obtained from the first two runs, $n = 6$ plants.

smallest (<1%) relative increase in vegetative biomass in response to elevated CO₂ by the time of flowering (Table 3). Variation in leaf area among cultivars is due to different flowering times as a consequence of maturity group (see Table 1). Stem weight showed the greatest relative sensitivity to elevated CO₂, increasing an average of 57% for all cultivars. No consistent stimulation of root weight or root/shoot ratio was observed among cultivars in response to elevated CO₂. Initial vegetative harvests at 10 DAS indicated a significant effect of CO₂ treatment on biomass for Harrow, Manchu, and Mukden, but no other cultivars (data not shown).

All cultivars showed a significant increase in seed yield with elevated CO₂ with an average response of about 40%; although variation in the response of yield to elevated CO₂ was obvious between experimental runs (Fig. 1). However, for each run, Mandarin showed the largest response of seed yield when compared with all

Table 3. Growth characteristics at initial flowering of nine soybean cultivars grown at either ambient (40 Pa) or elevated (71 Pa) carbon dioxide partial pressure. Data are means for three experimental runs.

Cultivar	CO ₂	Leaf area	Leaf weight	Stem weight	Root weight	TOTAL weight
	Pa	cm ² plant ⁻¹	g plant ⁻¹			
Arksoy	40	3335	6.54	5.02	2.17	13.73
	71	3371	7.75	7.27*	2.28	17.30
CNS	40	5603	11.17	9.94	2.56	23.67
	71	6930*	17.12*	15.87*	4.84*	37.82*
Dunfield	40	3429	7.20	6.84	2.05	16.09
	71	4459*	11.19*	11.08*	3.22*	25.46*
Harrow	40	1778	4.05	2.89	1.45	8.38
	71	2251*	7.03*	5.64*	2.57*	15.24*
Manchu	40	2078	4.63	3.63	1.26	9.52
	71	2793*	6.31*	6.02*	1.67*	13.99*
Mandarin	40	2098	5.43	4.62	2.13	12.19
	71	2691*	7.30*	6.56*	2.46	16.33*
Mukden	40	2285	6.08	4.95	1.98	13.02
	71	3070*	8.93*	8.14*	3.01*	20.08*
S-100	40	3292	8.11	7.41	2.43	17.99
	71	4509*	11.64*	12.22*	3.64*	27.48*
Williams	40	2864	7.86	6.10	3.19	17.14
	71	3045	7.80	6.74	2.55	17.10

* Indicates a significant difference ($P < 0.05$) relative to ambient CO₂ within a cultivar.

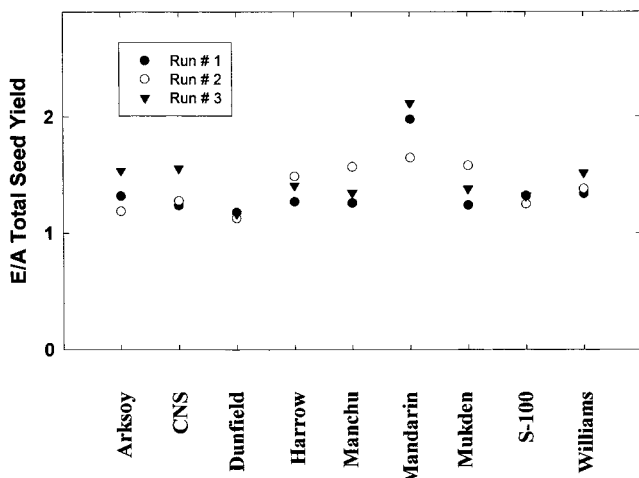


Fig. 1. Variation in the ratio of seed yield (g plant^{-1}) at elevated (71 Pa, E) to that at ambient (40 Pa, A) carbon dioxide for eight ancestral and one modern soybean cultivar over three runs of the experiment. To test for differences among cultivars in the responsiveness of seed yield to elevated CO_2 , the ratio of the mean value at elevated (E) to that at ambient CO_2 (A) for a given experimental run was calculated. Variation among cultivars in this ratio was tested using one way ANOVA, with three replicates. The mean seed yield response of Mandarin was significantly ($P = 0.05$) higher than the other cultivars. Cultivars are listed alphabetically.

other cultivars. Overall, the response of Mandarin was significantly greater than those of the remaining cultivars ($\sim 2\times$, Fig. 2). No significant differences in the relative response of seed yield was observed among the remaining cultivars (Fig. 2).

Among specific reproductive characteristics, elevated

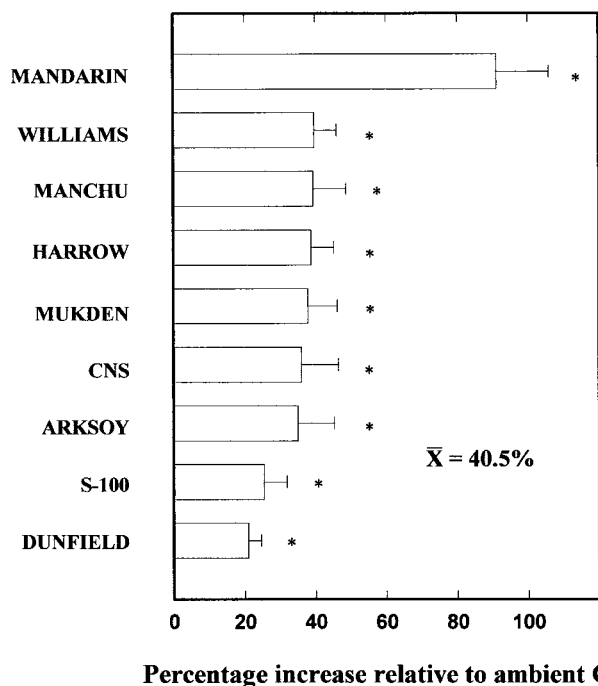


Fig. 2. The percentage stimulation of seed yield for nine soybean cultivars grown at elevated CO_2 (71 Pa, E) relative to the ambient CO_2 treatment (40 Pa, A) over three runs of the experiment. Cultivars are listed according to the relative response of seed yield to elevated CO_2 . * indicates a significant difference ($P < 0.05$) relative to ambient CO_2 for individual cultivars. Bars are $\pm \text{se}$.

CO_2 increased pod number, pod weight (pod wall and seed) and average weight of individual seed for most cultivars. However, negative effects on AHI and pods per node were also observed (Table 4). Although Mandarin showed the largest relative increase in seed yield, the largest absolute response was observed for Williams (Table 4).

When compared among cultivars, vegetative parameters obtained at flowering were poor predictors of seed yield sensitivity to elevated CO_2 (Table 5). As might be expected, reproductive characteristics at maturity, especially pod weight, were better predictors of seed yield sensitivity (Table 5). Interestingly, the response of seed yield to elevated CO_2 did not result in a similar increase in the amount of seed produced by main stem and axillary branches. Rather, the ability of a cultivar to produce branch seed was significantly correlated with its overall ability to respond to elevated CO_2 (Fig. 3). In contrast, while increases in main stem seed was observed with some cultivars, this did not correlate with the overall response of seed yield to CO_2 (Fig. 3).

DISCUSSION

Although the photosynthetic response to CO_2 was not determined after flowering, photosynthetic response and carbohydrate content during early vegetative growth and at the time of flowering should be a key determinant of flower number and pod set. The continued photosynthetic stimulation (i.e., no acclimation) observed here has been reported previously in soybean in response to elevated CO_2 (Campbell et al., 1990; Ziska et al., 1998). However, in the current experiment, photosynthetic response (either in absolute or relative terms) was not an accurate predictor of the seed yield response to CO_2 for the first two experimental runs ($r = 0.25$). Differences in whole plant or canopy photosynthesis could provide a more accurate assessment of the photosynthetic response. Previous studies with soybean have shown differences in the photosynthetic response of whole plants and single leaves in response to increasing CO_2 (Ziska and Bunce, 1997). However, while whole-plant photosynthesis could be a more accurate predictor of whole-plant soybean growth and reproductive sensitivity; pragmatically, only a small number of cultivars could be screened.

If photosynthetic response is not correlated with yield sensitivity among cultivars, then photosynthetic partitioning may be a more relevant parameter. In the current study, the vegetative response at flowering was not a good predictor of seed yield sensitivity to elevated CO_2 . In addition, partitioning among vegetative structures (e.g., specific leaf weight, root to shoot ratio, leaf to stem ratio) or changes in determinacy or maturity group (i.e., time to flowering), were also not correlated with the relative sensitivity of seed yield to elevated CO_2 (data not shown).

As might be expected, measurements made at maturity were better predictors of seed yield sensitivity. It is not surprising that increased pod weight was associated with increased seed yield at elevated CO_2 . What is some-

Table 4. Reproductive characteristics of nine soybean cultivars grown at either ambient (40 Pa) or elevated (71 Pa) carbon dioxide partial pressure. Data are means of three experimental runs.

Cultivar	CO ₂	Pods/node	Pod no.	Total pod weight	Wt./Seed	Seeds/pod	Seed yield	AHI†
	Pa		No. plt ⁻¹	g plt ⁻¹	mg seed ⁻¹	No. pod ⁻¹	g plt ⁻¹	
Arksoy	40	2.1	103	49	174	1.8	30.8	0.58
	71	2.0	119	66*	216*	1.7	42.4*	0.57
CNS	40	1.9	149	83	182	1.7	45.6	0.50
	71	2.1	175*	117	211*	1.7	60.3*	0.52
Dunfield	40	2.0	98	63	232	2.0	46.1	0.64
	71	1.9	122*	81	230	1.9	55.9*	0.56*
Harrow	40	1.5	74	49	210	2.1	32.7	0.59
	71	1.5	92*	69*	225*	2.2	45.1*	0.57
Manchu	40	1.8	75	48	229	2.1	35.1	0.67
	71	1.6*	103*	74*	226	2.1	48.8*	0.58*
Mandarin	40	1.7	81	44	210	1.8	31.3	0.60
	71	1.7	115*	84*	248*	1.9	58.4*	0.57
Mukden	40	2.0	87	55	228	1.9	41.4	0.60
	71	1.6*	115*	86*	252*	1.9	56.5*	0.53*
S-100	40	1.9	140	80	162	2.1	46.0	0.56
	71	1.6*	130	93	202*	2.3*	60.0*	0.52*
Williams	40	1.6	80	66	224	2.6	46.0	0.66
	71	1.5	92	91*	264*	2.6	64.8*	0.62

* Significant difference ($P < 0.05$) relative to ambient CO₂ within a cultivar.

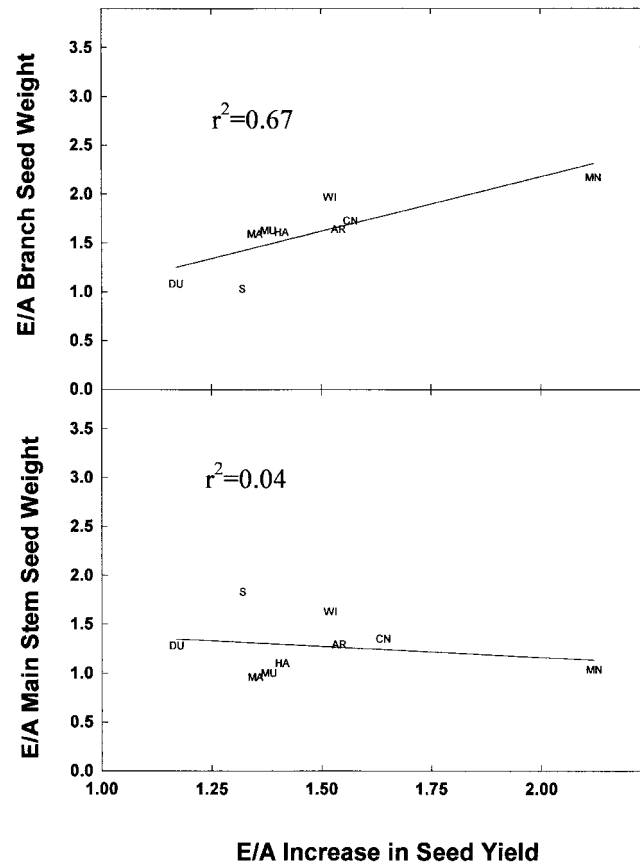
† Apparent harvest index.

what surprising, however, is that the increase in seed yield was not evenly distributed between main stem and axillary seed production. Seed yield sensitivity to CO₂ was related to the ability to produce additional seed on axillary branches. Increased axillary branching in response to elevated CO₂ also showed a good correlation with seed yield sensitivity ($r = 0.57$), but the correlation was not significant ($P = 0.10$). The situation observed here is somewhat analogous to that observed in field-grown rice in that branching (or tillering) is correlated with the ability of seed yield to respond strongly to elevated CO₂ (Moya et al., 1998).

If a cultivar such as Mandarin shows promise in the glasshouse, will it perform equally well in the field? Clearly, the response of single plants may differ from that of large scale canopies. Changes in planting density may be especially crucial if, in fact, axillary branching is required to optimize seed yield response. Yet, because

Table 5. Correlations between the relative increase in seed yield with elevated CO₂ and the relative change in other growth characteristics measured at flowering or at maturity for nine soybean cultivars.

Parameter	Correlation Coefficient†	Probability
<i>Characteristics at Flowering</i>		
Leaf Area, cm ² plant ⁻¹	0.31	0.595
Leaf Weight, g plt ⁻¹	0.14	0.716
Stem Weight, g plt ⁻¹	0.09	0.809
Root Weight, g plt ⁻¹	0.31	0.418
Total Weight, g plt ⁻¹	0.17	0.653
<i>Characteristics at Maturity</i>		
Pods per node	0.38	0.310
No. of Pods, plt ⁻¹	0.56	0.120
Pod Weight, g plt ⁻¹	0.89	0.001
Branch Seed‡, g plt ⁻¹	0.82	0.015
Main Stem Seed‡, g plt ⁻¹	0.22	0.393
Weight per seed, mg seed ⁻¹	0.17	0.658
Seeds per pod	0.43	0.247
Stem Weight, g plt ⁻¹	0.35	0.352
Branching, no. plt ⁻¹	0.58	0.104

† $n = 27$.‡ Data for Run 3 only, $n = 9$.**Fig. 3.** Change in the ratio of branch and main stem seed weight per plant at elevated (71 Pa, E) to that at ambient (40 Pa, A) carbon dioxide in relation to the increase in total seed yield for the entire plant. r^2 was significant for the change in branch seed weight per plant. AR = Arksoy; CN = CNS; DU = Dunfield; HA = Harrow; MA = Manchu; MN = Mandarin; MU = Mukden; S = S-100; WI = Williams. Data are from Run 3. Each point is the average of five plants.

the cost of screening large numbers of cultivars to CO₂ in the field remains prohibitive, glasshouse trials may serve as an initial step in determining variation and seed yield sensitivity to CO₂. Recent work with a modern soybean cultivar, Spencer, suggests that in some cases, glasshouse screening for yield sensitivity to rising CO₂ can transfer to field conditions (Ziska and Bunce, 2000). Obviously, confirmation of such an approach will require additional field studies of promising cultivars observed in the glasshouse.

This does not mean that all glasshouse observations should be dismissed. For example, in the current study, elevated CO₂ significantly reduced AHI in some cultivars. This indicates that, in general, vegetative growth is more sensitive to increases in CO₂ than reproductive development as has been observed previously for soybean in the field (e.g., Baker et al., 1989). The current study also suggests that the reduction in AHI may occur in part because elevated CO₂ can also reduce key reproductive parameters. For example, the observed decline in AHI was associated with a reduction in the number of pods per node at elevated CO₂ for three of the four cultivars showing a significant reduction in AHI (Manchu, Mukden and S-100). The reduction in pods per node may have limited the relative increase in seed yield for these cultivars. Overall, no cultivar examined demonstrated an increase in either pods per node or seeds per pod (although there is a clear difference in seeds per pod between the modern cultivar Williams and ancestral lines). Presumably, maintaining or increasing these parameters (in addition to increasing pod number, average seed weight, etc.), could result in a greater stimulation of both relative seed yield and potentially, AHI in a field trial.

CONCLUSIONS

Clearly, any organized effort to utilize genotypic variation to increase seed yield in soybean or other important agronomic plants as atmospheric CO₂ increases, is still in its initial stages. We recognize that experiments examining genotypic variation in a glasshouse may not always mimic larger scale responses in the field. However, because of the high costs associated with maintaining an elevated CO₂ environment, it is difficult to determine the full range of genotypic variability for large numbers of cultivars using a traditional field approach. On the basis of these initial results, there appears to be significant variation in the sensitivity of seed yield to elevated CO₂ among ancestral soybean cultivars. While the stimulation of photosynthesis remains the driving force for increases in growth and yield in response to elevated CO₂, variation in either the absolute rates or relative degree of stimulation was not associated with the observed sensitivity of seed yield reported here for soybean. Vegetative response or differences in vegetative partitioning among organs at flowering was also poorly correlated with seed yield variation. Interestingly, one factor which may predict seed yield sensitivity is seed production on axillary branches. Overall, data

from the current study demonstrate that there is significant variation in seed yield sensitivity among soybean cultivars, and that such sensitivity may be associated with plasticity related to the production of axillary branches and additional seed production at a future, elevated level of carbon dioxide.

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Genetic Improvement in Short Season Soybeans: I. Dry Matter Accumulation, Partitioning, and Leaf Area Duration

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ABSTRACT

Genetic improvement of short-season soybean [*Glycine max* (L.) Merr.] cultivars has resulted in a 0.5% annual gain in yield. Although yield is the product of dry matter (DM) accumulation and partitioning, the relative contributions of these two components of yield to genetic improvement has not been documented. Furthermore, the mechanism by which higher DM accumulation or harvest index (HI) is accomplished in the newer cultivars is unclear. The objective of the current study was to characterize DM accumulation and partitioning in cultivars which differ in yield potential, and determine the role of these traits in yield improvement. Two older (low yield potential) and two newer (higher yield potential) soybean cultivars of similar maturity were grown in side-by-side trials in 1996 and 1997. Plant samples were taken during each growing season and separated into leaves, stems + petioles, roots, and seeds. Dry matter accumulation and leaf area indices were measured. Seed yield of the new cultivars was 30% greater than their older counterparts. Increased DM accumulation contributed 78% and increased HI contributed 22% towards the genetic gain in yield. Total plant dry weight increased to a maximum around R4/R5 and subsequently declined during the seed-filling period (SFP) as pod development increased and leaf senescence began. This decline in dry weight during the SFP was greater for the old than for the new cultivars. The newer cultivars maintained leaf area further into the SFP than the old cultivars enabling continued dry matter accumulation. The results of this experiment indicate that genetic yield improvement in the short-season soybean cultivars examined was mainly associated with longer leaf area duration and the subsequently greater DM accumulation.

GENETIC IMPROVEMENT in yield for short- and long-season soybean cultivars from USA and Canada has been reported to be in the range of 0.5 to 1% annually (Luedders, 1977; Wilcox et al., 1979; Specht and Williams, 1984; Voldeng et al., 1997). The average soybean yield in Ontario increased linearly between 1942 and 1997 from approximately 1200 to 2600 kg ha⁻¹ (Anon, 1999). Such yield increases may be due to either improved agronomic practices or improved soybean genetics (genetic gain) or the interaction of genetic gain and enhanced agronomic practices as cultivars are selected under new management practices (Evans, 1993).

Voldeng et al. (1997), in a test of 41 soybean cultivars (0 and 00 maturity groups) released over 58 yr, found an accelerating rate of yield improvement, suggesting an increasingly important role of genetic gain in the continued efforts to maintain yield improvement.

Grain yield is the product of total DM and HI and can therefore be affected by either change in HI, or a change in DM accumulation, or both. The main breeding challenge in short-season soybean areas is to maximize DM accumulation within the short growing season while allowing for seed maturation to occur before frost.

Most of the early investigations into soybean yield improvement have revealed little evidence for the role of partitioning (HI). In tests on soybeans of different growth habits and yield potential, no evidence was found that HI and improved yield potential were correlated (Schapaugh and Wilcox, 1980; Cregan and Yaklich, 1986). In more recent studies, however, HI has been reported to be a significant contributor to yield improvement (Frederick et al., 1991; Shiraiwa and Hashikawa, 1995; Morrison et al., 1999). The contradictory nature of the reports on HI and yield bring to question the relative contribution of partitioning to soybean yield improvement.

Research on the association between DM accumulation and soybean yield have also reported contradictory results. In early research, no association between DM accumulation and yield were found (Shibles and Weber, 1965; Weber et al., 1966). These researchers used different planting patterns and populations to increase DM accumulation. The treatments they imposed affected DM accumulation predominantly during the vegetative period. A more recent study of four Japanese soybean cultivars reported that difference in DM accumulation between old and modern genotypes was most apparent after the beginning of the SFP (Shiraiwa and Hashikawa, 1995). The contradictory finding in earlier and more recent studies may be evidence of a temporal relationship between DM accumulation and yield improvement.

A number of researchers have attempted to identify critical periods for soybean yield determination (Egli, 1988; Board and Harville, 1993; Hayati et al., 1995; Board et al., 1996). Investigations on the vegetative period have reported no evidence to link either DM accumulation during the vegetative period or the duration

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Abbreviations: CAP, canopy apparent photosynthetic rate; CER, carbon exchange rate; CGR, crop growth rate; DM, dry matter; HI, harvest index; EEf, effective filling period; LAI, leaf area index; MG, maturity group; SFP, seed-filling period; SGR, seed growth rate.